

TAXONOMIC OVERVIEW OF *EURYBIA* SECT. *HERRICKIA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Herrickia horrida and five closely related species are included here within *Eurybia* sect. *Horrida*. These species are *E. glauca*, *E. horrida*, *E. pulchra*, and *E. wasatchensis*, as previously treated by Nesom, and two other species recently recognized by molecular evidence as close relatives: ***Eurybia kingii*** (D.C. Eat.) G.L. Nesom, comb. nov. (including ***Eurybia kingii*** var. ***barnebyana*** (Welsh & Goodrich) G.L. Nesom, comb. nov.) and ***Eurybia aberrans*** (A. Nels.) G.L. Nesom, comb. nov. The first five of these species were treated by Brouillet as a broadened genus *Herrickia*; the last was segregated as the monotypic genus *Triniteurybia* Brouillet, Urbatsch & Roberts. Molecular data indicate that *Eurybia*, *Herrickia*, and *Triniteurybia* constitute a 3-taxon grade at the base of the Machaerantherinae clade but morphological distinctions of *Herrickia* and *Triniteurybia* from *Eurybia* are trivial or non-existent and their separation from *Eurybia* at generic rank is based strictly on cladistic hypotheses. Nomenclatural summaries and geographic distributions are shown for the six species of *Eurybia* sect. *Herrickia*.

RESUMEN

Herrickia horrida y cinco especies muy relacionadas con ella se incluyen aquí en *Eurybia* sect. *Horrida*. Estas especies son *E. glauca*, *E. horrida*, *E. pulchra*, y *E. wasatchensis*, tal como habían sido tratadas previamente por Nesom, y otras dos especies reconocidas recientemente mediante pruebas moleculares como parientes próximos: ***Eurybia kingii*** (D.C. Eat.) Nesom, comb. nov. (que incluye ***Eurybia kingii*** var. ***barnebyana*** (Welsh & Goodrich) Nesom, comb. nov.) y ***Eurybia aberrans*** (A. Nels.) Nesom, comb. nov. Las cinco primeras especies fueron tratadas por Brouillet como el género más amplio *Herrickia*; la última fue segregada como el género monotípico *Triniteurybia* Brouillet, Urbatsch & Roberts. Los datos moleculares indican que *Eurybia*, *Herrickia*, y *Triniteurybia* constituyen un grado de tres taxa en la base del clado Machaerantherinae pero las diferencias morfológicas de *Herrickia* y *Triniteurybia* con *Eurybia* son triviales o inexistentes y su separación de *Eurybia* en el rango genérico está basada estrictamente en hipótesis cladísticas. Se aportan resúmenes nomenclaturales y distribuciones geográficas para las seis especies de *Eurybia* sect. *Herrickia*.

Prior to 1994, *Herrickia horrida* Woot. & Standl. either had been maintained as a monotypic genus or treated as *Aster horridus* (Woot. & Standl.) Blake. Nesom (1994) united it with three morphologically similar species in the western U.S.A. and treated the group as sect. *Herrickia* (Woot. & Standl.) Nesom of the genus *Eurybia* (Cassini) S.F. Gray: *Eurybia glauca*, *E. horrida*, *E. pulchra*, and *E. wasatchensis*. *Eurybia* in the sense of the present overview includes a total of 28 species distributed over eastern and western North America.

Based on molecular study, Brouillet et al. (2004) reinstated *Herrickia* Woot. & Standl. at generic rank, including the species noted above but reducing *Eurybia pulchra* to varietal rank within *Herrickia glauca* and expanding the group to include *Aster/Tonestus kingii*. They also discovered *Haplopappus/Tonestus aberrans* to be a close relative of *Herrickia* and *Eurybia* and segregated it as the monotypic genus *Triniteurybia* Brouillet, Urbatsch & Roberts (Brouillet et al. 2004). Molecular evidence indicates that this group of “herrickioid” taxa forms a grade at the base of subtribe Machaerantherinae: *Oreostemma* (*Herrickia* (*Eurybia* (*Triniteurybia* (*Machaerantherinae*)))) (Brouillet et al. 2004, from ITS and 3’ETS nrDNA; Selliah and Brouillet 2007, from the nuclear CNGC4 gene). The boundaries of *Eurybia* were further adjusted with the transfer of *Eurybia* (*Aster*) *pygmaea* (Lindl.) Nesom and *Eurybia* (*Aster*) *chapmanii* (Torrey & A. Gray) Nesom to *Symphyotrichum* (Brouillet & Selliah 2005; Brouillet et al. 2006).

The taxonomic repositioning of *Symphyotrichum chapmanii* and *S. pygmaea* is justified, based on molecular as well as morphological criteria, and those two species are outside of the immediate relationship of the species of *Herrickia*/*Eurybia*/*Triniteurybia*. The inclusion of *Aster kingii* and *Haplopappus aberrans* in this group of species also is a valuable and morphologically justified insight. The implicit rationale of strict monophyly, however, for recognizing three separate genera among these few species of the eurybioid grade

is based on a philosophical position not universally shared by systematists (e.g., Nordal & Stedje 2005), whether or not further molecular data may confirm the pattern of cladistic relationship among them. There is no consistent, diagnostic morphological difference to separate *Herrickia* (sensu Brouillet) from *Eurybia*, and *Triniteurybia* is distinguished from *Herrickia* and *Eurybia* by a single feature (lack of ray florets), which is sometimes variable within species and at most no greater than sometimes differentiating species among genera of Machaerantherinae sensu stricto. Of course, as among species, there are no consistent or objective criteria specifying the number or kinds of differences that justify the recognition of closely related genera (or see McVaugh's set of recommended criteria [1945]). Similarly, however, there is no constraint that the pattern of descent be mirrored in nomenclature that does not account for phenotypic modification (or lack of it). Were *Herrickia*, *Eurybia*, and *Triniteurybia* distinguished by significant morphological features, combined with a preliminary cladistic hypothesis, their treatment as separate genera would certainly be justified.

The present overview examines the generic concepts of *Herrickia*, *Eurybia*, and *Triniteurybia* and shows geographical distributions of species included here within *Eurybia* sect. *Horrida*. Map data are taken from specimens at ASC, BRIT-SMU, MO, SJC, and TEX-LL.

Morphological distinction of *Herrickia* from *Eurybia*

Eurybia (sensu Nesom 1994, 2000) is distinctive in its combination of corymboid inflorescence, ciliate-fringed, rounded phyllaries with a green, often basally truncate apical patch, linear-lanceolate disc style appendages, cylindric and multinerved cypselae, 2-seriate pappus of equal-length, apically thickened bristles, and base chromosome number of $x = 9$. Brouillet et al. (2004, 2006) did not provide morphological criteria for the distinction of *Herrickia* from *Eurybia*, but for the FNANM treatment, the key to genera (FNANM Editorial Committee 2006, p. 19) used the following contrast.

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|--|------------------|
| 1. Stems and leaves usually stipitate-glandular, sometimes eglandular and glaucous; leaves mostly cauline, entire or spinulose-serrate, glabrous or scabrellous; phyllaries sometimes rounded, usually keeled, apices acute to long-acuminate; rays 8–27; disc corolla tubes shorter than limbs (w Cordilleras) | Herrickia |
| 1. Stems and leaves usually eglandular, sometimes stipitate-glandular (e North America only), not glaucous; leaves basal and/or cauline, serrate (teeth sometimes spinulose or spinose, blades then linear, grass-like, se North America) or entire, hairy or glabrous; phyllaries usually rounded, sometimes keeled, apices obtuse to acute; rays 5–60; disc corolla tubes shorter or longer than limbs | Eurybia |

Each of the comparisons in the key shows broadly overlapping characters and there is no consistent, diagnostic morphological difference to separate *Herrickia* (sensu Brouillet) from *Eurybia*.

My rationale for the recognition of sect. *Herrickia* (Nesom 1994) was similarly lacking in diagnostic cohesiveness, reflecting more a perception of the geographical coherence of the species. *Eurybia horrida* and *E. wasatchensis* are similar in their subshrubby habit, sessile and subclasping leaves, subequal phyllaries, and tendency to produce foliaceous bracts immediately subtending the involucre. *Eurybia glauca* and *E. pulchra* are similar to the former two in habit and subclasping leaves but differ in graduate phyllaries and lack of foliaceous bracts. Only the subshrubby habit is distinct among other species of the genus and *E. glauca* and *E. pulchra* sometimes are more herbaceous than subshrubby. *Tonestus aberrans* and *Aster kingii* are similar between themselves (see comments below) and both show features of *Eurybia*, but they are distinct from other “herrickioids” in their herbaceous habit and reduced inflorescence; both produce non-clasping leaves and graduate phyllaries, and they lack foliaceous bracts. Thus, there apparently is no obvious morphological feature diagnostic of the herrickioid group, but the seemingly interrelated species clusters and their geographic coherence (Figs. 1 and 2) suggest that they are closely related within the larger *Eurybia*, and molecular data tentatively confirm this.

Morphological distinction of *Eurybia* and *Triniteurybia*

In the original description of *Triniteurybia* as a new genus (Brouillet et al. 2004), its diagnostic features were noted (in the Latin diagnosis only, as differences from *Eurybia*) as eradiate heads and stipitate-glandular leaves. The western U.S.A. species *Eurybia integrifolia* and *E. conspicua*, however, have stipitate-glandular foliage, as does *Herrickia* (*Eurybia*) *horrida*. *Herrickia glauca* var. *pulchra* (= *Eurybia pulchra*), *Herrickia* (*Eu-*

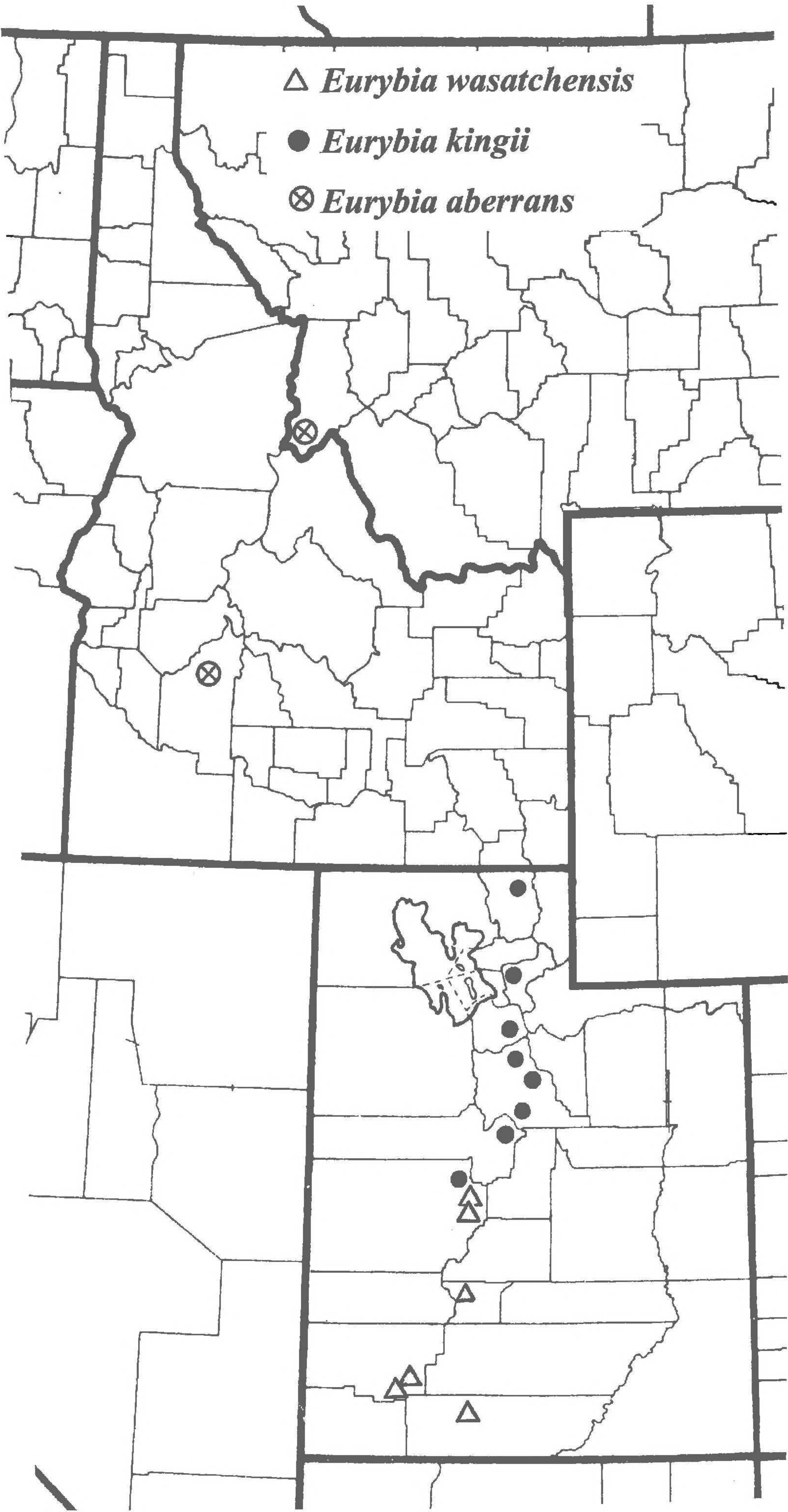


FIG. 1. Distribution of *Eurybia wasatchensis*, *E. kingii*, and *E. aberrans*.

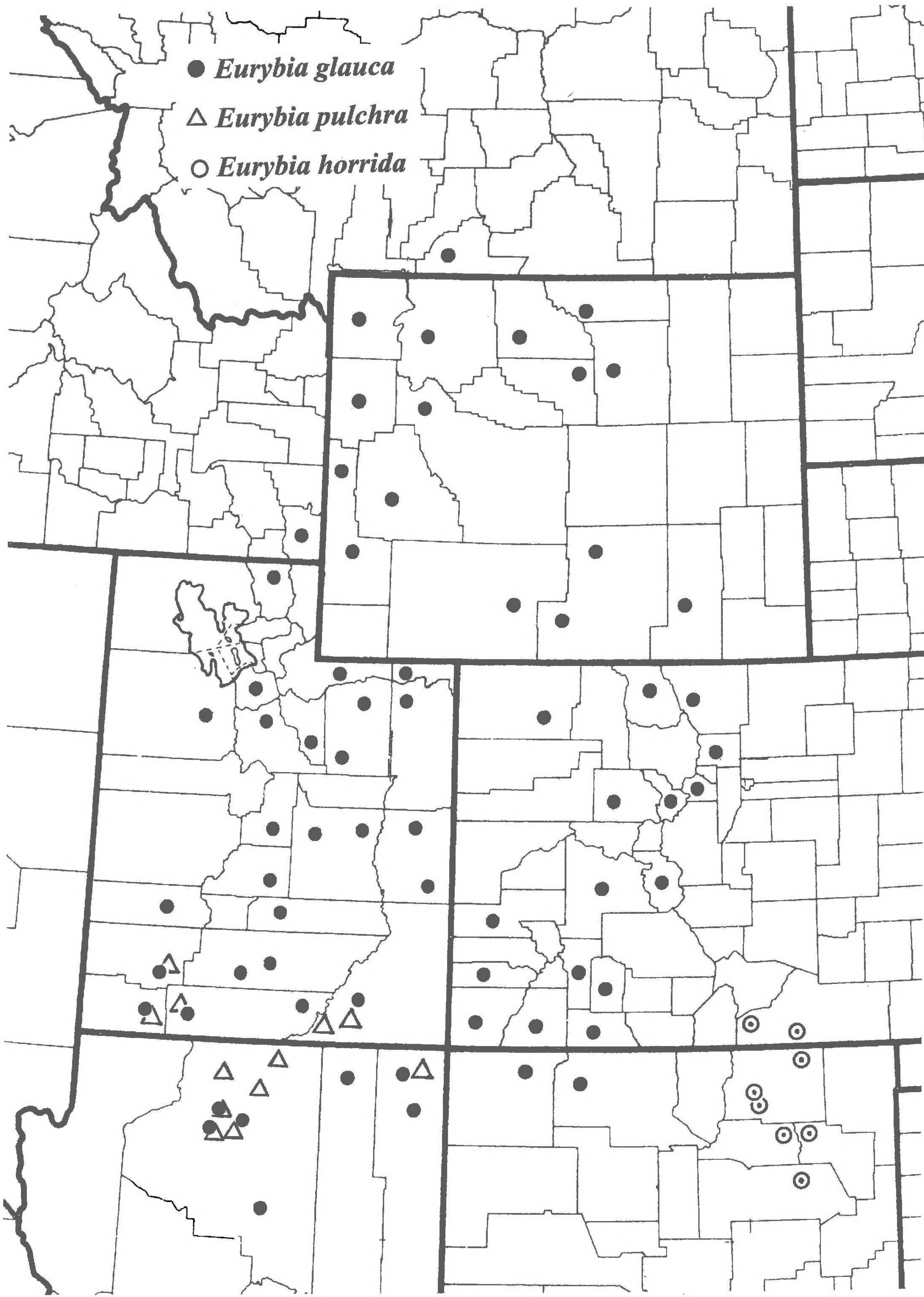


FIG. 2. Distribution of *Eurybia glauca* and *E. pulchra*, and *E. horrida*. The record for *E. pulchra* in Iron Co., Utah, is based on the citation by Welsh (2003).

rybia) *wasatchensis*, and the recently joined *Herrickia kingii* have stipitate-glandular stems, peduncles, and phyllaries. Distal leaves of *H. kingii* sometimes are minutely stipitate-glandular (e.g., *Smith* 3508, TEX, from Box Elder Co., Utah). Some species of *Eurybia* in the eastern U.S.A. also produce stipitate-glandular vestiture: e.g., *E. macrophylla*, *E. schreberi*, *E. spectabilis*. In summary, the vestiture of *Triniteurybia aberrans* is not distinct among its close relatives. Brouillet later observed (2006, p. 364) that stipitate-glandularity “is most likely a shared primitive feature within [*Herrickia*] and is therefore not indicative of a particular relationship within the group.”

In the FNANM treatment of *Triniteurybia*, Brouillet (2006, p. 382) observed that “the cylindro-campanulate heads with imbricate phyllaries and a wide green area, and the coarse, dentate foliage, are similar to those of *Eurybia*. The lack of ray florets clearly distinguishes *Triniteurybia*.” In fact, lack of rays has been the only morphological feature noted in any discussion that is diagnostic of the new genus. *Triniteurybia aberrans* is the only rayless species in the eurybioid grade, but within subtribe Machaerantherinae sensu stricto, *Dieteria canescens* is variable in ray production, *Arida carnosa* is rayless, and *Xanthisma grindelioides* is rayless. Ray production also is variable among species of *Grindelia*. Lack of ray florets may justify recognition of a taxon at specific rank, but there is no other example in the Astereae where it is the sole morphological character for distinction of a genus.

Eurybia kingii* and *Eurybia aberrans

In the positioning of *Aster kingii* within *Tonestus* (Nesom 1991), the species was noted (p. 124) to be most closely similar to *Tonestus aberrans*: “Indeed, as a pair the two are somewhat set apart from the rest of the genus in the toothed leaves often with spinulose teeth, narrowly lanceolate-attenuate and apically spreading or reflexed phyllaries, style appendages with more widely arranged sweeping hairs, and purplish disc corolla lobes.” And (p. 125) “in spite of its white rays, it fits more securely in [*Tonestus*] than in *Aster*, particularly when placed next to *T. aberrans*.” Molecular evidence confirms that the two are closely related, and their morphological and geographical similarity (Fig. 1) support this hypothesis. Both are treated here within *Eurybia*.

Taxonomic status of *Aster glaucodes* subsp. *pulcher* Blake

Nesom (1994) treated *Aster glaucodes* subsp. *pulcher* at specific rank within *Eurybia*, as *E. pulchra*, distinct from *E. glauca*. *Eurybia pulchra* “differs from *E. glauca* in its smaller leaves, apically acute phyllaries, and well-developed glandularity. ... *Eurybia pulchra* has a restricted geographic range, and in the specimens I have examined, there appears to be no intermediacy between it and *E. glauca*” (p. 194). The present study shows that *E. pulchra* (northern Arizona and southern Utah) is sympatric with the more widespread *E. glauca* (Fig. 2) and confirms a paucity of intermediates between them. Plants of *E. pulchra* have distal stems, peduncles, and phyllaries densely stipitate-glandular, while those of *E. glauca* are completely glabrous.

Numerous collections of both taxa have been made in the Grand Canyon, in the area of Havasupai Canyon and roughly between Havasupai Canyon and Bright Angel Canyon, e.g.: ***Eurybia glauca***: *Clover* 4513, 5136, 7018 (LL), *Deaver* 1524, 2135, 2677, 2944, 3053 (ASC), *Hodgson* 16026 (ASC); ***Eurybia pulchra***: *Clover* 7189 (LL), *Deaver* 3042 (ASC), *Rink* 4455, 4477a (ASC), *Stevens* s.n. [14 Aug 1992], s.n. [27 Sep 1992] (ASC). Among all plants I have studied, the only three that might suggest the possibility of gene flow are from this area: *Watters* 26 (ASC) and *Deaver* 4412 (ASC) are typical *E. glauca*, except that the peduncles of each are minutely and sparsely glandular for about one centimeter immediately below the heads; *Stevens* s.n. [10 Apr 1991] (MO) is glabrous except for sparsely glandular distal peduncles and glandular phyllary margins.

A putative distinction noted by Brouillet et al. (2006) in number of disc florets (12–32 in *Eurybia glauca*, 29–40 in *E. pulchra*) is not confirmed here, as *E. pulchra* has florets evenly distributed in number down to at least 19. Leaf and phyllary morphology also overlap, though *E. pulchra* does tend to have slightly smaller leaves and more acute phyllaries. Within the area of sympatry, differences in habitat and phenology are not apparent.

In his decision to treat *Eurybia pulchra* at varietal rank within *E. glauca*, Brouillet (2003, p. 1561) noted that “the ranges of the two taxa appear to be parapatric in southern Utah-northern Arizona, with *E. pulchra* restricted to the vicinity of the Grand Canyon while *E. glauca* ranges widely to the north and east into the Southern Rocky Mountains; it must be noted however, that populations of the latter are found in Arizona south and east of the Grand Canyon. Nonetheless, no mixed population of the two taxa has been reported. The restricted range and distinct glandularity justify that *E. pulchra* be recognized as a taxon. Nevertheless, glandularity alone does not seem to justify recognizing *E. pulchra* as a distinct species.” Brouillet’s observation that the lack of glands in *E. glauca* represents a derived condition is reasonable and probably correct but in itself not pertinent to the decision of rank. The contrasting observation here that the ranges are sympatric suggests that the distinct polarity in vestiture is maintained through genetic isolation, in which case specific rank for each entity is justified. It is possible that in the southern part of the range (the range of *E. pulchra*), some kind of genetic switching turns on or off the expression of glands, but similar variation does not occur within other taxa of sect. *Herrickia* or any other *Eurybia* species. If *E. pulchra* is to be recognized at any rank above “forma,” the behavior of these two taxa as distinct species is the simplest hypothesis as the basis for assignment of rank. Field study clearly is needed.

Welsh (2003) recognized the distinctiveness of *Eurybia puchra* and treated it as a variety of *E. wasatchensis* rather than a closer relative of *E. glauca*. The implication by Brouillet et al. (2006) that *E. pulchra* and *E. glauca* are sister taxa is better supported by morphology.

TAXONOMIC SUMMARY OF EURYBIA SECT HERRICKIA

Eurybia sect. **Herrickia** (Woot. & Standl.) Nesom, *Phytologia* 77:258. 1994. *Herrickia* (Woot. & Standl.). *Triniteurybia* Brouillet, Urbatsch & Roberts, *Sida* 21:898. 2004.

Lack of a clear diagnosis for the herrickioid group, apart from the seemingly interrelated species clusters and the geographic coherence of the species, renders the formal recognition of sect. *Herrickia* weakly justified. Nevertheless, it is a useful category in reference to the group.

- 1. **Eurybia aberrans** (A. Nels.) G.L. Nesom, comb. nov. BASIONYM: *Macronema aberrans* A. Nels.; *Haplopappus aberrans* (A. Nels.) H.M. Hall; *Sideranthus aberrans* (A. Nels.) Rydb.; *Tonestus aberrans* (A. Nels.) Nesom & Morgan; *Triniteurybia aberrans* (A. Nels.) Brouillet, Urbatsch & Roberts.
- 2. **Eurybia glauca** (Nutt.) Nesom, *Phytologia* 77:260. 1994. *Eucephalus glaucus* Nutt.; *Herrickia glauca* (Nutt.) Brouillet; *Aster glaucus* (Nutt.) Torrey & A. Gray 1841 (non Nees 1818); *Aster glaucodes* Blake.
- 3. **Eurybia horrida** (Woot. & Standl.) Nesom, *Phytologia* 77:260. 1994. *Herrickia horrida* Woot. & Standl.; *Aster horridus* (Woot. & Standl.) Blake.
- 4. **Eurybia kingii** (D.C. Eaton) G.L. Nesom, comb. nov. BASIONYM: *Aster kingii* D.C. Eaton in S. Watson, *Botany* (Fortieth Parallel) 141, plate 16, figs. 1–6. 1871. *Machaeranthera kingii* (D.C. Eaton) Cronq. & Keck; *Tonestus kingii* (D.C. Eaton) Nesom; *Herrickia kingii* (D.C. Eaton) Brouillet, Urbatsch & Roberts.
- 4a. **Eurybia kingii** (D.C. Eaton) G.L. Nesom var. **barnebyana** (Welsh & Goodrich) G.L. Nesom, comb. nov. BASIONYM: *Machaeranthera kingii* var. *barnebyana* Welsh & Goodrich, *Brittonia* 33:299, fig. 5. 1981. *Aster kingii* var. *barnebyana* (Welsh & Goodrich) Welsh; *Tonestus kingii* var. *barnebyana* (Welsh & Goodrich) Nesom; *Herrickia kingii* var. *barnebyana* (Welsh & Goodrich) Brouillet, Urbatsch & Roberts.
- 4b. **Eurybia kingii** (D.C. Eaton) G.L. Nesom var. **kingii**
- 5. **Eurybia pulchra** (Blake) Nesom, *Phytologia* 77:261. 1994. *Aster glaucodes* subsp. *pulcher* Blake; *Aster glaucodes* var. *pulcher* (Blake) Blake; *Aster wasatchensis* var. *pulcher* (Blake) Welsh; *Eurybia glauca* var. *pulchra* (Blake) Brouillet; *Herrickia glauca* var. *pulchra* (Blake) Brouillet.
- 6. **Eurybia wasatchensis** (M.E. Jones) Nesom, *Phytologia* 77:262. 1994. *Aster glaucus* var. *wasatchensis* M.E. Jones; *Aster wasatchensis* (M.E. Jones) Blake; *Eucephalus wasatchensis* (M.E. Jones) Rydb.; *Herrickia wasatchensis* (M.E. Jones) Brouillet.

CONCLUSION

While the overall understanding of the herrickioid group is essentially the same as that of Brouillet et al.

(2004) and Brouillet (2006), the taxonomic alternative proposed here conveys an equally or more useful picture of the evolutionary standing of these species. Treating them within *Eurybia*, while explicitly pointing out evolutionary relationships suggested by the cladistic hypothesis, emphasizes their morphological similarity and geographic coherence. The Brouillet et al. taxonomy emphasizes the evolutionary discreteness of species that are morphologically inseparable by characters used elsewhere in the tribe and family to distinguish genera. The formal recognition of a paraphyletic group at generic rank, compared to the cladistically-derived alternative, has merit in this extreme example where morphology plays essentially no role at all in the classification. Further research may resolve the issue with less ambiguity.

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